DISTRIBUTION OF FRESHWATER SNAILS: SPATIAL SCALE AND THE RELATIVE IMPORTANCE OF PHYSICOCHEMICAL AND BIOTIC FACTORS

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ABSTRACT

Traditionally, freshwater snail distributions have been explained as the result of physicochemical factors, especially calcium concentration. Yet factors operating on different spatial and temporal scales rarely have been stated explicitly and alternate explanations have not been explored thoroughly. In the following conceptual model, we suggest that different factors govern snail species composition and abundance across different spatial scales. Across biogeographic boundaries, water chemistry screens potential colonists, with some species not persisting where calcium levels are less than about 5 $mg \cdot l^{-1}$. Given adequate calcium, abundance and distribution of species among and within water bodies within a region are determined by available habitats and food, if levels of disturbance, competition, and predation are low. In temporary ponds, disturbance lowers species richness and competition. Predators such as fish and crayfish determine snail abundance and species composition among and within most permanent lakes.

In support of this perspective, we provide preliminary data from three geographic areas on two spatial scales, among and within lakes, to document the importance of disturbance, competition, food selection, and predation in structuring freshwater snail assemblages. In northern Indiana, disturbance and predation seem most important in determining snail assemblages across lake types. Within a permanent pond in southern England, snail distribution depends on disturbance and food selection. Finally, distribution and abundance of snails and predators in a large permanent lake in northern Wisconsin suggest the importance of habitat-mediated predation by sunfish, crayfish, and leeches. We are now testing the predictions of this conceptual model using laboratory selection experiments, field-cage studies, and extensive lake surveys.

Freshwater ecologists (Boycott, 1936; Macan, 1950; Russell-Hunter, 1978, Økland, 1983) traditionally have stressed the importance of calcium in determining distribution and abundance of freshwater snails. Most authors have arrived at this emphasis after studying lakes in contiguous and geologically uniform regions: the English Lake District (Boycott, 1936; Macan, 1950); the Scottish lochs (Russell-Hunter, 1978); southern Finland (Aho, 1966, 1978a, b, c;

Aho et al., 1981); and Norway (Økland, 1983). Poor in calcium-bearing rocks, these regions are dominated by soft-water lakes. Owing to a concentration of this regional approach in soft-water areas, it is not surprising that effects of calcium, i.e. absence or low abundance of snails in low calcium lakes, was noticed and stressed. Yet, among lakes with abundant snails, the variation in distribution and abundance of various species remains unexplained. We believe that ecological studies at both wider (among regions) and narrower (within water bodies) spatial scales provide a more comprehensive explanation of snail distribution and abundance. In this paper, we first review briefly the literature on the importance of water chemistry in snail ecology. We then present a statistical analysis of published data sets on snail distributions and lake characteristics in northern Wisconsin that indicates water chemistry does not adequately explain snail distributions. Finally, we generate a conceptual model, with preliminary supporting examples, that suggests the importance of abiotic factors (calcium and disturbance) and biotic factors (habitat and food selection, interspecific competition, disturbance, and especially predation) in determining among- and within-lake abundances of snails.

THE TRADITIONAL VIEW

The traditional view of snail ecology, as summarized above, implies the overriding importance of calcium, but to suggest previous authors have ignored other factors would be unfair. Russell-Hunter (1978), for example, thought that trophic state, in conjunction with calcium, primarily influenced the distribution of snails, whereas water temperature was secondary, and the role of dissolved oxygen was uncertain. Although Jokinen (1983) suggested that biotic factors be tested to determine their influence on snail diversity and abundance, dissolved minerals remain the most studied factors despite evidence that water chemistry, at best, poorly predicts species composition, abundance (Harman and Berg, 1971), and shell calcification.

Calcification is not related to calcium concentration in any simple way (Morrison, 1932; Burky et al., 1979; Nduku and Harrison, 1980a; Russell-Hunter et al., 1981). Though Michigan lakes with thick-shelled Physa integra Haldeman have thick-shelled Helisoma anceps (Menke) and those with thin-shelled P. integra have thin-shelled H. anceps, shell thickness and environmental calcium are not correlated (Hunter and Lull, 1977). There is a similar lack of correlation between shell calcium concentration and environmental calcium in other regions (Mackie and Flippance, 1983a,b; McMahon, 1983).

Though the exact interaction between calcium and snail abundance is unknown, calcium still provides insight into snail distributions. Aho (1966) found species in calcium-poor lakes that were previously thought to require much greater calcium (Boycott, 1936). Although Dussart (1976, 1979a,b) found species abundances related to water hardness, Økland (1983) found that gastropod diversity declined significantly only in lakes with extremely low calcium concentrations (< 5.2 mg Ca·l⁻¹). Even given this result, at least some

species thrive in very softwater lakes; Rooke and Mackie (1984) found dense Amnicola limosa (Say) populations in soft-water (< 3 mg Ca·l⁻¹) Canadian lakes. Systematic changes in gastropod assemblages occur across geologic interfaces of soft- and hard-water Canadian lakes and streams (McKillop and Harrison, 1972; McKillop, 1984). Using stepwise multiple regression, McKillop (1984) found concentrations of calcium, nitrate, and nitrite best predicted snail species abundances. Such findings, however, leave causality in question. The value of calcium, nitrate, and nitrite as predictors may result from positive correlations with lake productivity. These field correlational studies suggest that for some species in some regions, very low calcium can limit successful colonization once dispersal has occurred.

Both laboratory and field experiments (Williams, 1970; Thomas, 1973; Thomas et al., 1974; Young, 1975; Nduku and Harrison, 1976, 1980b; Dussart and Kay, 1980) suggest a minor ecological role for calcium except at extremely low levels (< 4.5 mg·l⁻¹) when snails are adversely affected physiologically. Clearly, at calcium levels above about 5 mg·l⁻¹, other factors determine snail distribution and abundance.

Among other physicochemical factors, water temperature and oxygen seem most important. Temperature determines onset and termination of reproduction in most freshwater snails (Russell-Hunter, 1978) as well as developmental rates, fecundity, and voltinism patterns (Brown, 1979; McMahon and Payne, 1980; El-Emam and Madsen, 1982; McMahon, 1983). High ambient temperatures may even limit the geographical distribution of some species (Van der Schalie and Berry, 1973). Low oxygen levels may preclude some prosobranchs (Aldridge, 1983; McMahon, 1983) and the ability of pulmonates to use atmospheric oxygen provides a clear advantage in hypoxic situations (Cantrell, 1981).

In summary, most of the above mentioned studies suggest that physicochemical factors set biogeographic limits to species distributions. Biotic factors, in turn, are probably more important in determining among- and within-lake abundances (see Green, 1971; Dillon and Benfield, 1982).

## SNAIL ASSEMBLAGES IN NORTHERN WISCONSIN LAKES

To evaluate the importance of abiotic variables on the distribution of snails, we analyzed previously published data sets on snail occurrences (Morrison, 1932) and physicochemical parameters (Black et al., 1963; Andrews and Threinen, 1966) for 64 northern Wisconsin lakes. As many as 20 snail species from the entire pool of 35 species were found in any one lake. Lakes varied in size from 4.5-2,080 ha and had alkalinities of 1.5-81 mg·l⁻¹.

Although number of species was positively correlated with maximum depth, shoreline length, alkalinity, and conductivity, these correlations may be explained by well known species-area relationships (MacArthur and Wilson, 1967; see also Lassen, 1975; Aho, 1978a,b,c; Browne, 1981; Brönmark, 1985b for biogeographic treatments of snail distributions), given that these factors were positively correlated to surface

area. However, in a stepwise multiple regression analysis, only two of the variables, area and alkalinity, were included in the regression equation (Table 1). To investigate the importance of alkalinity when the effect of area was accounted for, we analyzed the relationship between the species-area residuals (i.e. the portion of the number of species in a lake that remains unexplained by the species-area regression) and alkalinity. A significant ($p < 0.001$), positive relationship existed between the species-area residuals and alkalinity (Fig. 1), which means that in lakes of equal size, those with a higher alkalinity had a higher number of snail species. Although this can indicate the importance of calcium in determining snail distributions, the ultimate factor could be lake productivity or some other factor correlated with alkalinity. Further, the regression only explains a small part of the variability ($R^2 = 0.19$), indicating that other factors such as biotic interactions can be important in determining snail distributions. In addition, when comparing lakes with different alkalinities we found no obvious trend in the distribution of snail genera, other than that lakes with alkalinity less than 10 mg·l^{-1} (about

3 mg Ca·l^{-1}) seemed to have a depauperate snail fauna (Fig. 2). Thus biotic factors are the most likely explanation for the
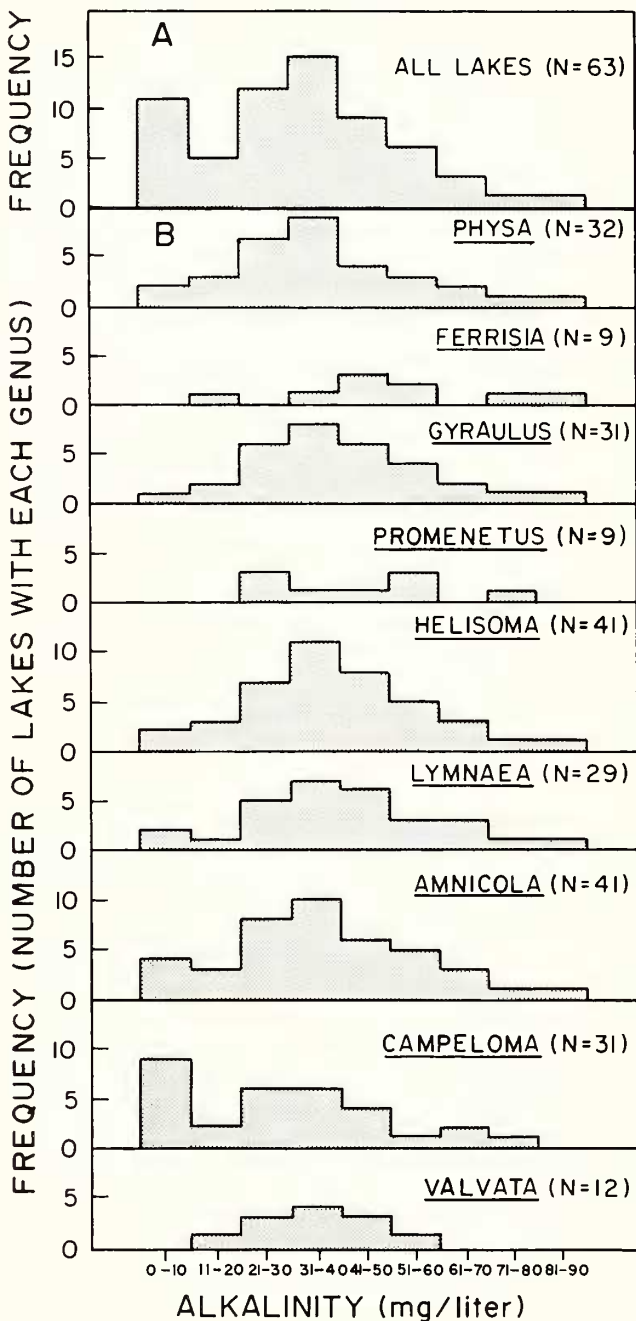
Table 1. Stepwise multiple regression analysis of physicochemical parameters (from Black et al., 1963; Andrews and Threinen, 1966) and number of snail species (from Morrison, 1932) occurring in lakes in northern Wisconsin.

Variable	B	Sum of squares	F	P
Area	0.004	228.7	16.2	< 0.001
Alkalinity	0.105	207.7	14.7	< 0.001
Intercept	0.504			
	$R^2 = 0.42$			
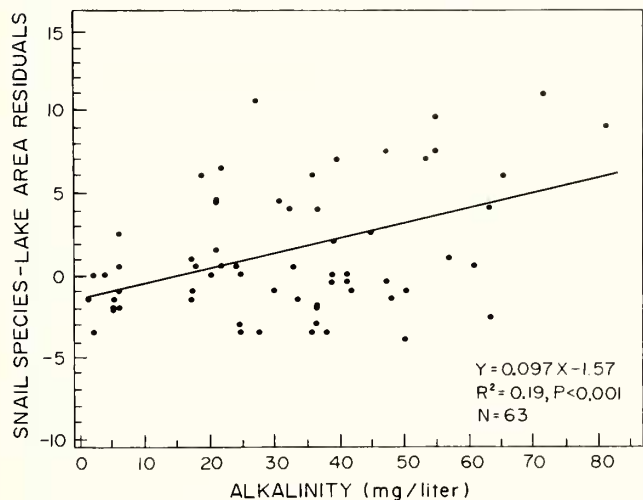
**Fig. 1.** Regression of snail species-lake area residuals (S*) on lake alkalinity.

Fig. 2. (A) Alkalinity distribution of all lakes included in multiple regression analysis of lakes and snails in northern Wisconsin and **(B)** alkalinity distribution of lakes containing each of nine snail genera. Recent simultaneous measurements of alkalinity and calcium (Northern Lakes Long Term Ecological Research project, J. J. Magnuson, Center for Limnology, University of Wisconsin-Madison) in four of the lakes included in this analysis suggests that 10 mg alkalinity·l^{-1} (as measured by Black et al., 1963) equals 3 mg Ca·l^{-1}.

distributions of snails among lakes of northern Wisconsin and in other lake regions, especially where calcium concentrations lie above 1-5 mg·l^{-1}.

A NEW CONCEPTUAL MODEL

We suggest that ecological forces act on different spatial scales and vary in importance in different water bodies. Below, we introduce those ecological factors we expect to be important across three spatial scales: (1) biogeographic scale, among geographic regions; (2) within geographic regions, among water bodies; (3) within water bodies, among habitats. We treat each of these spatial scales across the habitat continuum from temporary ponds to permanent lakes (Fig. 3). We then provide examples from our work that elucidate the relative importance of ecological factors in controlling snail assemblages among and within water bodies.
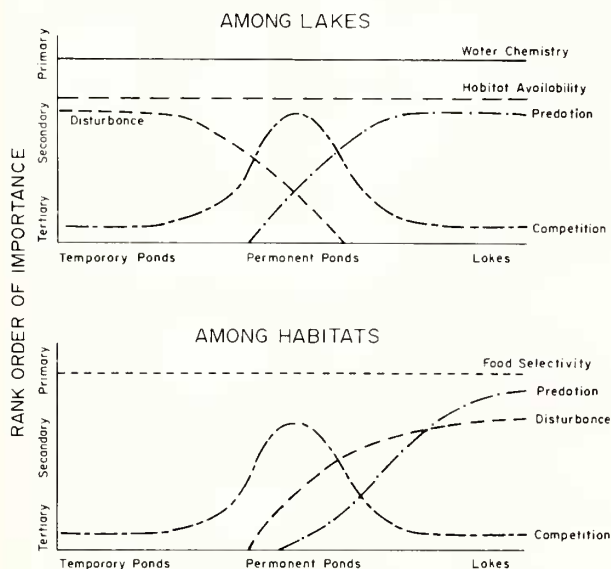
Fig. 3. Conceptual model of the importance of physicochemical and biotic factors in determining the distribution and abundance of freshwater snails on two spatial scales. The factors important in determining snail distribution and abundance in any given lake type (temporary pond, permanent pond, lake) should be understood as a heirarchy. Among habitats within a lake, for example, we expect that if food selectivity by snails does not explain the snails' distribution and abundance, then predation is the next most likely explanation. If predation is not the most important factor, then disturbance or competition probably is. A graph for "Among Regions" is not shown because we expect water chemistry is the over-ridingly important force determining differences in snail abundance on that spatial scale. Such a graph would simply have a straight horizontal line for "Water Chemistry."

COLONIZATION AND THE INFLUENCE OF WATER CHEMISTRY

The biogeographic, evolutionary history of a region determines the potential pool of snail colonizers. Several mechanisms of dispersal of freshwater snails apparently ensure colonization opportunities for all snails among water bodies within a region (e.g. Lassen, 1975). However, as reviewed above, snails cannot colonize if calcium concentration are less than 5 mg·l^{-1}. Such filtering of colonizers probably occurs across regions and to a degree within regions of very soft-water lakes.

HABITAT AND FOOD SELECTION

If calcium is adequate for snail survival, then productivity and habitat diversity of lakes may determine density and species richness within a region (Russell-Hunter, 1978). In turn, available habitat types can interact with species-specific preferences for habitat and food to determine within-lake patterns. For example, snail species diversity and substrata complexity (including macrophytes) are positively correlated in freshwater lakes of central New York (Harman, 1972). Such a relationship probably results from habitat preference (e.g. Ross and Ultsch, 1980). Macrophytes, in particular, often support a rich gastropod fauna, with snail-macrophyte associations general in some cases (Soszka, 1975; Mason, 1978; Lamarche et al., 1982; Aldridge, 1983) and specific in others (Calow, 1973a; Pip and Stewart, 1976; Pip, 1978, 1985; Lodge, 1985, 1986). For ponds in southern Sweden, snail species richness and macrophyte species richness are positively correlated (Brönmark, 1985). In one case at least, specific macrophyte-snail associations result from food choice among different periphyton assemblages occurring on different macrophytes (Lodge, 1985, 1986).

Because the preferred diets of most snail species are unknown (see Calow, 1970, 1973a,b; Calow and Calow, 1975; Reavell, 1980), few predictions about specific habitat-snail associations can be made. Yet when food preference data are available, they are good predictors of species abundances in different habitats. For example, snails that prefer detritus in laboratory trials, are common in wooded ponds whereas species preferring algae are dominant in open ponds (Brown, 1982). Thus substrata and feeding preferences influence snail assemblage structure among and within lakes.

DISTURBANCE

The temporal availability of appropriate habitat and food may be critical to species persistence. Habitat disturbance (Pickett and White, 1985) can eliminate those species less able to rapidly recolonize from refuges and reproduce. Seasonal drying of temporary ponds (Brown et al., 1985) and winterkill (hypoxia under ice) can be important and widely occurring sources of mortality. Snail populations also decline dramatically following reductions in macrophytes (Pimentel and White, 1959; Lodge and Kelly, 1985). Waves on exposed lake shores can also reduce snail populations much as waves on marine rocky intertidal habitats reduce the abundance of organisms (Sousa, 1984). Because such disturbances typically affect only parts of lakes or, at their broadest scale, several lakes within a region, they can contribute to the variation in snail assemblages among lakes and to differential species distributions within lakes. Rarely would local disturbances contribute to differences in snail fauna among regions.

COMPETITION

Traditionally, competition has been invoked as the major structuring force in natural communities. However, this perspective has recently been a major point of controversy, with much older evidence for competition and character displacement being called into question (e.g. Strong et al., 1984). Disturbance can keep many communities in a non-equilibrium state. In such communities, population densities can never reach levels at which resources are limiting. Even in near equilibrium communities, however, predation can be the dominant structuring force (Connell, 1975). Such mechanisms clearly reduce competition in many systems (Denslow, 1985).

Laboratory experiments suggest the potential for competition among marine and freshwater snails (Fenchel and Kofoed, 1976; Madsen, 1979; El-Emam and Madsen, 1982), but field evidence is rare (Eisenberg, 1966) and anecdotal. Fenchel (1975) predicted that divergence in shell size of sympatric congeneric marine hydrobiids reduced food resource overlap. However, Levinton (1982) was unable to show differences in resource use among different sizes of hydrobiid snails. Brown (1982) investigated overlap patterns in an assemblage of four pond snails in the American midwest and found considerable divergence among species in feeding and habitat use patterns. Of the six possible pairwise interactions, overlap was high in only one. Yet even those two species inhabited temporary ponds where populations suffered dramatic mortality each year (Brown et al., 1985); habitat lifespan may not have been long enough for interspecific competition to become an important structuring force.

Wiens (1984) argues that for a better understanding of important structuring factors, a spectrum of communities from non-equilibrium to equilibrium should be studied. The continuum from small temporary ponds to large permanent lakes constitutes such a set of communities. We predict that among and within water bodies, disturbance and predation reduce snail populations below densities at which competition would be important. Interspecific competition would be a major influence in permanent water bodies, and then only where other forces do not limit population size or distribution.

PREDATION

Predation is an important source of mortality for marine (Ebling et al., 1964; Kitching et al., 1966; Spight and Lyons, 1974; Spight, 1976; Vermeij, 1978, 1979; Palmer, 1979, 1985; Vermeij and Currey, 1980) and freshwater molluscs (Eisenberg, 1966; Gillespie, 1969; Covich, 1976, 1981; Vermeij and Covich, 1978). Marine snails have evolved thick, elaborately sculptured shells to deter their predators (Vermeij, 1978; Vermeij and Covich, 1978; Palmer, 1979, 1985; Bertness et al., 1981). Although most freshwater snails have not coexisted with their predators for as long (Vermeij and Covich, 1978), large species with thick, strong shells have an advantage against predation over small, thin-shelled species (Stein et al., 1984; Brown and Devries, 1985). The presence of an operculum in the prosobranchs also can serve as a defense, especially against shell-invading predators (Brönmark and Malmquist, 1986; Brown and Strouse, unpubl. data). The

evolutionary significance of predation is further supported by the existence in some thin-shelled pulmonates of escape behaviors, e.g. shell shaking (Townsend and McCarthy, 1980) and leaving the water when attacked by leeches (Brönmark and Malmquist, 1986).

We expect the importance of predation to increase directly with water body size and permanence. Major predators of snails in temporary ponds are shell-invading invertebrates, e.g. sciomizid fly larvae (Eckblad, 1976), dytiscid beetles and belostomatid bugs (Eisenberg, 1966), odonates, flatworms (see Reynoldson and Piearce, 1979), and leeches (see Davies et al., 1981; Young, 1981). Few data are available on the distribution patterns and predation rates of these small invertebrate predators, but most probably have low predation rates relative to those of large, shell crushing decapod crustacean and fish predators. For example, individual leeches eat fewer than one snail per night (Brönmark and Malmquist, 1986; Brown and Strouse, unpubl. data). The hemipteran *Belostoma* eats up to 10 snails per night and can dramatically reduce the populations of temporary pond snails (Kesler, pers. comm.). Individual crayfish and sunfish can eat > 100 snails·day^{-1} (Covich and Klosiewski, unpubl. data). Along the continuum from temporary ponds to lakes, small invertebrate predators with low predation rates can be replaced by more effective decapod crustacean and fish predators. In a later section, we present data that suggest predation often determines among- and within-lake snail species distributions.

PARASITISM

Larvae of digenic trematode helminths are common parasites of both pulmonate and prosobranch snails (Holmes, 1983). Trematode infections can initially increase the growth rates of individual snails, but eventually depress growth and reproduction; snails with mature infections (shedding cercaria) are castrated (Wright, 1966; Hairston, 1973; Brown, 1978; Minchella and LoVerde, 1981; Minchella et al., 1985). Therefore, infections can alter population dynamics, but little information is available on infection levels in natural populations of freshwater snails. Nothing is known of the effects of trematode parasites on the competitive abilities or predator avoidance abilities of freshwater snails. In populations of pulmonate pond snails in Indiana, prevalences are about 25%, and increase dramatically with the length of the snail life cycle. Under such conditions, trematodes could reduce the population growth rates of snails (Brown et al., unpubl. data).

However, in Trout and other lakes in the north central lake district of Wisconsin, prevalence (percentage of sampled individuals shedding cercaria) for most snail species was < 5% (Table 2). Because only these individuals are castrated, the effect on population dynamics is probably minor. However, because some species of snails (Table 2) do harbor large populations of metacercaria (resting cysts that can reinfect the same or different snail species), longer term studies of trematode dynamics in snails are necessary. Because prevalences were low for most of these lake-dwelling

Table 2. Prevalence of larval trematodes in snails in several Vilas County, Wisconsin lakes. Snails were collected in June 1984 and July 1985, isolated for 24 h at 700 footcandles, examined for emerging cercaria (C), and then crushed to recover metacercaria (M). For each snail species, trematode types are listed in order of abundance.

Species (Lake)	Year	(N)	Occurence of Trematodes (%) Cercaria	Metacerc.	Trematode Type
Lymnaea emarginata (Say)	1984	(30)	22.2	100.0	Diplostomatid (M)
(Trout)	1985	(105)	3.8	0.0	Echinostome (C), Strigeid (C), Xiphidis (C)
L. stagnalis (Linn.) (Trout)	1984	(30)	0.0	100.0	Strigeid (M), Echinostome (M), Tetracotyl (M)
	1985	(67)	0.0	10.4	Tetracotyl (M)
Helisoma anceps	1984	(30)	0.0	10.0	Echinostome (M)
(Trout)	1985	(61)	4.9	0.0	Echinostome (C), Xiphidis (C)
Physa spp.	1984	(30)	0.0	0.0	
(Trout, Mann)	1985	(73)	5.5	0.0	Schistosome (C)
Gyraulus parvus (Say) (Trout, Mann)	1985	(73)	6.8	30.2	Strigeid (C,M)
Amnicola limosa (Trout)	1985	(104)	0.0	0.0	
Campeloma decisa (Trout, Grassy)	1985	(95)	25.3	94.5	Cyathocotylidae (C), Xiphidis (C), *Leucochloridismorpha constantiae* Gower (C,M)

snails, we suggest that parasitism is not an important population regulating factor for most species in large permanent bodies of water.

THE MODEL REVISITED

In summary, we predict that water chemistry acts as a filter for colonists and probably contributes to differences in snail fauna across broad geographic boundaries. Given adequate calcium, quantity and quality of available habitat and food determines abundance and distribution of species if disturbance and predation are low. Especially in temporary ponds, disturbance keeps diversity and interspecific competition at low levels. Competition is most likely to occur in permanent water bodies where predation is low and exerted by relatively few, ineffective invertebrates. We view these conditions as somewhat special and predict that in most lake districts, more effective predators, especially crayfish and fish, are abundant and the most important source of snail mortality. The impact of predators will, however, be mediated by habitat structure. Below, we provide preliminary data on two spatial scales—among and within lakes—and from three geographic areas to document the importance of disturbance, competition, food selection, and predation in structuring freshwater snail assemblages.

AMONG LAKES: DISTURBANCE, COMPETITION, AND PREDATION

Along a gradient of temporary to permanent water bodies in northeastern Indiana, clear changes in species composition occur (Fig. 4). Pulmonates are abundant in temporary ponds and a permanent pond whereas prosobranchs are abundant in Crooked Lake, a large marl lake. These patterns are consistent with our conceptual model . Because temporary ponds are disturbance-dominated, only pulmonates that can aestivate during the annual drying cycle occur. When the pond refills, these pulmonates can repopulate, owing to their short generation times and high fecundities (see Calow, 1978; Browne and Russell-Hunter, 1978; Brown, 1983).

Prosobranchs, apparently unable to withstand dry periods, do not occur in temporary ponds. Yet alternate explanations for prosobranch absence exist: lack of colonization; competitive exclusion by pulmonates; and inappropriate physicochemical environment, especially periodic low oxygen. Although pulmonates possess characteristics that make them good "colonizers" (*sensu* Lewontin 1965), reaching a water body apparently is not a problem for any group of snails (see Jokinen, 1983). Rapid colonization of British waters by *Potamopyrgus jenkinsii* (Smith) (Bishop and DeGaris, 1976)
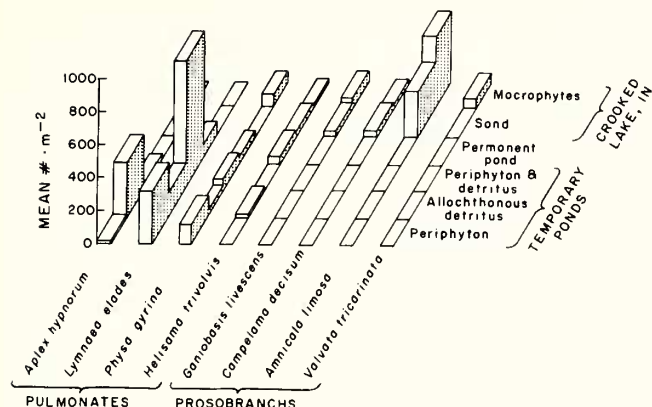
Fig. 4. Densities of snails in northeastern Indiana across water bodies differing in permanence, food resources, and predators. Temporary ponds drying earliest are at the bottom; ponds and within-lake habitats toward the top are more permanent. Fish predators occur only in the permanent pond and Crooked Lake. Snails were sampled with an Ekman grab (with minimum sample number = 10). Samples were pooled and sorted as described in Brown (1982). Ponds were sampled in June-July 1980, 1981; Crooked Lake was sampled in June-July 1983.

attests to the mobility of prosobranchs. In those prosobranchs that have life histories similar to pulmonates, populations can grow rapidly after disturbance (Lodge and Kelly, 1985). Because competition would have at most 1-3 generations during which to be effective in a temporary pond (except among those species surviving the dry period), competitive exclusion is unlikely. Finally, low oxygen could exclude prosobranchs from temporary and small eutrophic ponds. Unlike pulmonates, most of which can use atmospheric oxygen, prosobranchs are restricted to gill-breathing (see McMahon, 1983).

In temporary ponds, seasonal drying and low oxygen can exclude prosobranchs and allow pulmonates to flourish. In contrast, lake habitats, as more permanent water bodies, are generally more favorable to snails. If permanent habitats allow prosobranchs to flourish (Fig. 4), why are pulmonate densities often low? We believe that both competition and predation could be important. Unfortunately, mechanisms of competition between pulmonates and prosobranchs are not clear, and few relevant data are available.

Relative to prosobranchs, most pulmonates have a thin shell. Thus they are more susceptible to shell-crushing predators (Stein et *al.,* 1984), which are more abundant in permanent water bodies than in temporary ponds. The greater abundance of the pulmonate *Lymnaea elodes* Say in an unproductive temporary pond, relative to a productive permanent pond (Fig. 4), results from predation by the central mudminnow [*Umbra limi* (Kirtland)], which only occurs in the permanent pond (Brown and Devries, 1985). We suspect that both the general low abundance of pulmonates in permanent waters and the greater abundance of snails in general in macrophytes, relative to sand, are predator effects. In Crooked Lake (Fig. 4), pumpkinseed [*Lepomis gibbosus* (Linn.)] and

redear sunfish [*L. microlophus* (Gunther)], both specialist molluscivores (see Mittelbach, 1984; Stein et *al.,* 1984), were common (Brown, unpubl. data), but macrophytes probably act as a refuge from fish predation (Crowder and Cooper, 1982; Gilinsky, 1984).

WITHIN WATER BODIES: DISTURBANCE AND FOOD SELECTION

Distributions of snails between submerged and emergent macrophytes within Radley Pond, a 0.9 ha, eutrophic pond in southern England are influenced primarily by disappearance of submerged macrophytes (Lodge and Kelly, 1985) and by selection of periphyton foods between different macrophyte types (Lodge, 1985, 1986). Of six moderately abundant gastropods in Radley Pond, five have much higher numbers per m² bottom area in one habitat, i.e., either on submerged or emergent macrophytes (Fig. 5). Even if snail densities are expressed per unit surface area of macrophytes (as per Cattaneo and Carignan, 1983), such differences in densities (1-4 orders of magnitude) demonstrate that snail distributions are not simply a product of macrophyte abundance in the two habitats.

A summerkill of submerged macrophytes (Fig. 6) reduced dramatically the densities of those snails inhabiting them (Fig. 5) whereas emergent macrophytes and associated snails changed little. With regrowth of submerged macrophytes, previous patterns of distribution and abundance recurred (Figs. 5 and 6).

Those species that inhabited the submerged macrophytes generally had shorter life cycles and higher fecundities than the inhabitants of the emergent macrophytes (Lodge and Kelly, 1985). Interaction between life history characteristics and habitat disturbance explains the absence of species with low fecundity in submerged macrophytes, but does not explain the absence of those with colonizing traits from the more permanent habitat. At least for *Lymnaea peregra* (Müller) and *Planorbis vortex* (Linn.) (diet preferences within other species were not examined), preferences for the periphyton found on their respective macrophyte substrates explain their distribution (Lodge, 1985, 1986). Neither competition nor predation are necessary to explain observed distributions.

Though shell-crushing predators are absent from Radley Pond, both invertebrate and vertebrate predators occur there. *Glossophonia complanata* (Linn.), a snail-eating leech (Wrona et *al.,* 1981), is abundant, especially in the emergent macrophytes. The mean annual density ($x \pm 1SE$, n = 20 months) of adult leeches was $117 \pm 36 \cdot m^{-2}$ in submerged macrophytes and $182 \pm 24 \cdot m^{-2}$ in emergent macrophytes (Lodge, 1986). Yet little is known of its predation rates or the selectivity of its feeding (Brönmark and Malmquist, 1986). The only vertebrate predator of snails in Radley Pond is the brown trout (*Salmo trutta* Linn.), but thick emergent macrophytes and the shallow water in which they grow restrict trout to submerged macrophytes. Among the snails, trout eat almost exclusively *Lymnaea peregra* (Lodge, 1986), the most abundant species in the submerged macrophytes. Radley Pond, then, demonstrates that when the
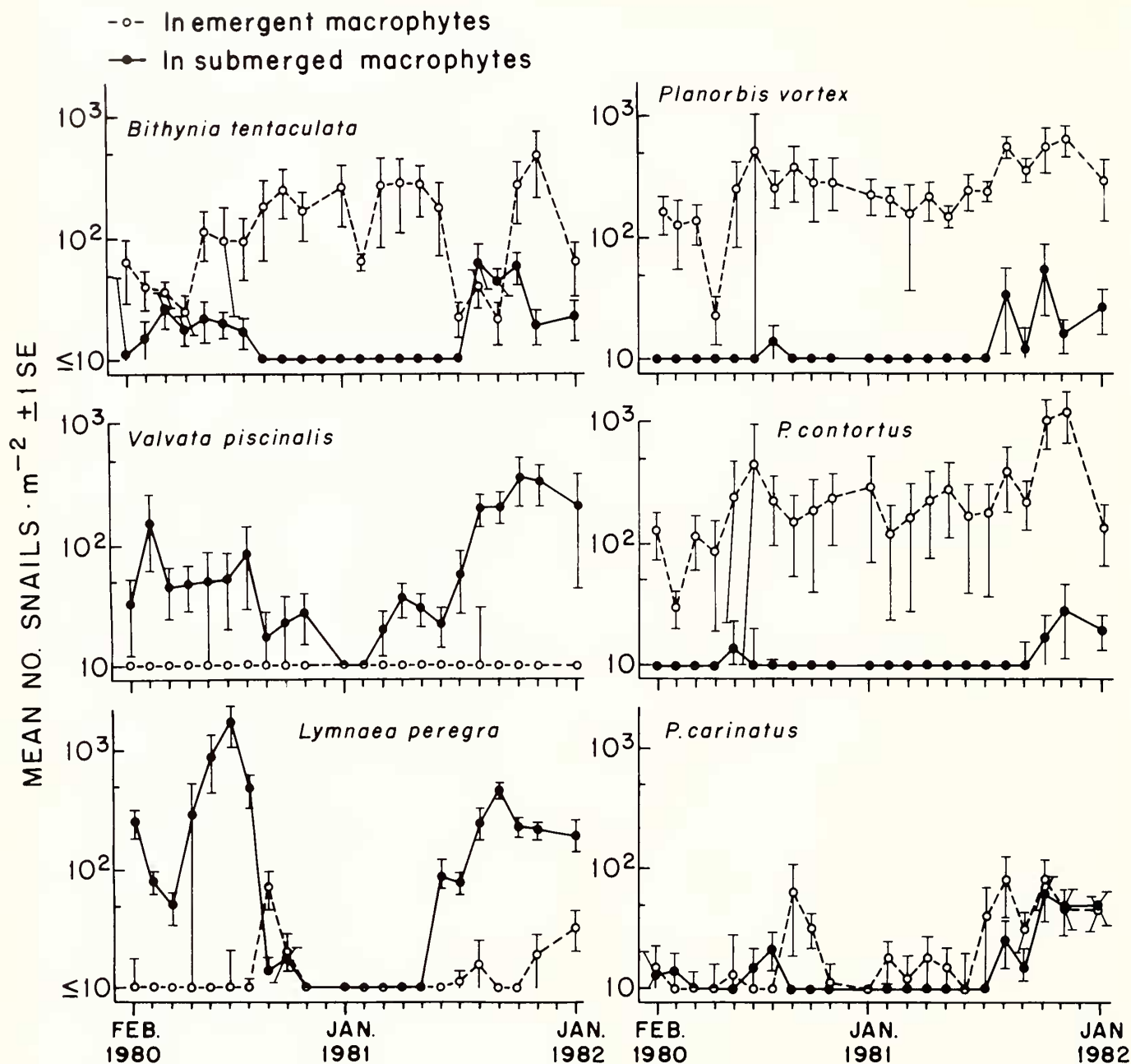
Fig. 5. Densities of snails in Radley Pond, southern England, in two neighboring macrophyte habitats, during 2 years. Submerged macrophytes were more permanent than emergent macrophytes and periphyton on the two macrophytes differed. Snails were sampled and sorted as described in Lodge (1985). Graphs for *Lymnaea peregra* and *Planorbis vortex* are taken from Lodge (1986).

magnitude of disturbance is relatively high, it has an important influence on the distribution of snails. Predation pressure is low in Radley Pond, and food preferences are expressed.

WITHIN WATER BODIES: PREDATION

We predict that in a large permanent lake with low disturbance, predation would be the major influence on snail

distributions (see Fig. 3). In Trout Lake, Wisconsin, neither summerkill nor winterkill occurs, and within-lake distributions of snails and predators were negatively correlated (Fig. 7). There were three potentially important predators types: pumpkinseed (sunfish), crayfish [*Orconectes rusticus* (Girard), *O. propinquus* (Girard), and *O. virilis* (Hagen)], and leeches [*Haemopis grandis* (Verrill)]. Small snails typically exceed 60% of the diet of adult pumpkinseeds (Sadzikowski and Wallace,
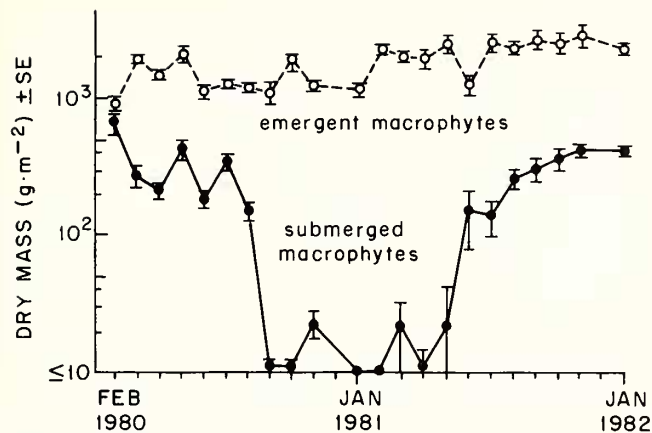
Fig. 6. Standing crop of two neighboring macrophyte habitats in Radley Pond during two years. Figure is taken from Lodge and Kelly (1985).

1976; Laughlin and Werner, 1980; Mittelbach, 1984). Crayfish are known to feed readily on snails (Covich, 1977). *H. grandis* is molluscivorous, but its distribution across habitats and feeding rates are poorly known. In Trout Lake, snail densities were highest on open sand substrates where food is apparently scarce, but crayfish and fish were virtually absent. In contrast, cobble habitats, where periphyton and crayfish were abundant, supported few snails (Fig. 7). Macrophyte habitats, where crayfish were intermediate in abundance and pumpkinseed were abundant (relative to other Trout Lake habitats), supported intermediate densities of snails. Although these preliminary data suggest that predators determine snail distribution across habitats within Trout Lake, alternate explanations, especially habitat selection by snails, and wave disturbance in cobble, certainly require testing.

SUMMARY

We have proposed a conceptual model of the factors important in determining the structure of freshwater snail assemblages. While colonization and water chemistry can be important in determining snail distribution across a large biogeographic scale, available evidence suggests disturbance and biotic factors are more important in determining distribution and abundance of snails among and within water bodies. Disturbance and its interaction with snail life histories is likely to be important among and within small water bodies. In the absence of disturbance and other constraints, habitat or food selection determines snail distributions among and within water bodies. Competition is likely to be important only in those few environments where predators are rare.

In permanent water bodies, predators can determine distribution and abundance of snails. Crayfish and fish, in particular, reach high densities in many lakes and have high feeding rates. Owing to the uneven distributions of predators across habitats within lakes, snails occur in habitats where predators do not occur, rather than in areas preferred by snails.
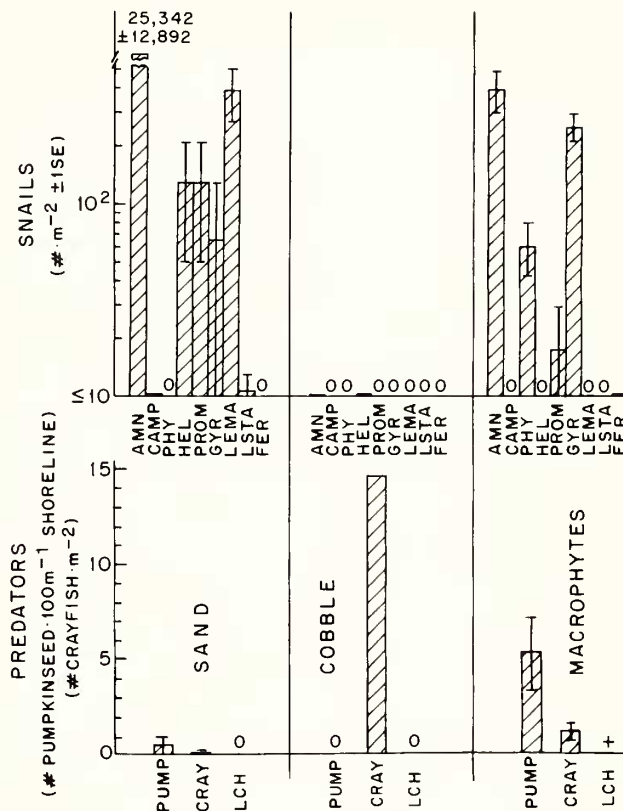

Fig. 7. Mean densities of snails and three types of snail predators (± 1 SE) in three neighboring habitats within Trout Lake, Wisconsin, June 1984. PUMP = *Lepomis gibbosus*, CRAY = *Orconectes* spp., LCH = *Haemopis grandis*; AMN = *Amnicola limosa*, CAMP = *Campeloma decisa*, PHY = *Physa* spp., HEL = *Helisoma* spp., PROM = *Promenetus exacuous*, GYR = *Gyraulus parvus*, LEMA = *Lymnaea emarginata*, LSTA = *L. stagnalis*, FER = *Ferissia* spp. Snails were sampled as follows [habitat, method (sample number)]: sand, 0.00307 m² cylindrical corer (5); cobble, 1 m² visual survey with SCUBA (5); macrophytes, 0.0127 m² cylindrical corer (18). Pumpkinseed abundance was determined by electrofishing two or three 100-m shoreline transects in each habitat. Crayfish in sand and macrophytes were counted visually in 1 m² quadrats (n = 5). Crayfish densities in cobble were taken from Capelli (1975). Relative abundance of leeches across habitats was estimated using SCUBA; plus (+) means relatively abundant, zero (0) relative rare. Biomass of macrophytes (predominantly *Potamogeton* spp., *Megalodonta beckii* (Torr.), *Vallisneria americana* Michx.) in macrophyte habitat was about 100 g dry mass·m⁻²; in sand habitat, biomass was about 10 g dry mass·m⁻² (predominantly *Isoetes* sp.).

Our conceptual model is largely consistent with available data. Most of these data are preliminary, and primarily meant to provide a basis for further work. Specifically, we require information on 1) feeding preferences and habitat choice by snails in the absence of predators, 2) snail choice and consumption rate of predators, and 3) the impact of parasitism. With these data in hand, sampling snails and predators across habitats within many lakes in a lake district will permit us to assess the validity of our conceptual model of snail distributional patterns.

ACKNOWLEDGMENTS

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